

MODIFICATION OF THE RESPONSES OF TWO SPECIES OF
BUGULA LARVAE FROM WOODS HOLE TO LIGHT AND
GRAVITY: ECOLOGICAL ASPECTS OF THE BE-
HAVIOR OF BUGULA LARVAE

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It is well known that the distribution of sessile organisms is markedly influenced by environmental conditions that affect the setting of their larvae. Thus, oysters are abundant at the mouths of certain rivers where their copper-laden waters are mingled with that of the ocean, and both maxima and minima of settings can be correlated with the amount of copper present during a critical stage of their development. (Cf. Prytherch, 1934.) Furthermore, rather frequent cases of co-occupation of a habitat by communities of sessile organisms of entirely different phyla would suggest the possibility that conditions favorable for the setting of one group are also advantageous to the other. The following observations on the effects of light and temperature on two species of *Bugula*, *B. flabellata* and *B. turrita*, from the Woods Hole region are presented partly because these factors influence distribution by affecting the attachment, metamorphosis and growth of the larvae and partly for the purpose of comparing and contrasting the behavior of these organisms with that of *B. ncritina*, formerly studied at Beaufort, North Carolina (Lynch, 1947). The problem of distribution of two species of the same genus is often a baffling one, as is well illustrated by the fact that *B. flabellata* and *B. turrita* occupy communicating waters not more than 100 yards from each other yet each is found almost exclusively in its own particular habitat. A better understanding of the physiology of the larvae may lead to the beginning of a solution of such problems of distribution.

Contrasting features of the larvae of B. flabellata and B. turrita

Since a description of the larva of *B. flabellata* and its reactions to light and gravity has been given by Grave (1930), only contrasting features of the two larvae or additional details of their behavior will be presented here. *B. flabellata*, the smaller of the two (average, 0.17 by 0.19 mm.), has ten or twelve flagella in its pyriform region and is devoid of light-reactive organs. *B. turrita* is larger (average, 0.19 by 0.20 mm.), has four or five long slender flagella and four brilliant-red, spherical eye-spots, two very close to the pyriform organ and two slightly larger ones located in the opposite hemisphere.¹ The whole body of the larva, except the eye-spots fluoresces faintly in ultra-violet light of 3600 Å. Ejected hold-fast material and disintegrated larvae, however, do not fluoresce. This response to

¹ It is difficult to understand why Grave (1930) referred to the light-receptive organs of the larva of *B. turrita* as being "darkly pigmented" and failed to mention their red color. Even with the light cut down to a minimum, their brilliance is an outstanding feature.

ultra-violet light seems to be caused by some substance in the integument of the larva. The cilia at the equator of both species are more active than those in other regions.

The taxonomy of the genus *Bugula* leaves much to be desired at the present time. In the position, color and shape of the eye-spots and in external structure the larva of American *B. turrita* is identical with that of the European *B. plumosa*, but the ground color of the former is yellow or flesh-colored (like that of the European *B. flabellata*), with a faint band of orange pigment at the equator, whereas that of *B. plumosa*, according to Nitsche (1870), is pure white. Furthermore, the larva of European *B. flabellata* differs from the American form, devoid of light receptive organs, since the former has ten symmetrically arranged eye-spots that are figured by Nitsche (1870) as slit-like or elongated and surrounded by fine cilia, but are ovoid according to Barrois' (1877) plates. Grave (1930) noted the difference between American and European species and stated that Calvét (1900) also referred to a confusion of varieties. Is the organism called *B. turrita* in America merely a variety of *B. plumosa*? Or is this a case in which evolutionary changes have affected only the larvae in some instances and only the adults in others? Since two species of *Bugula* sometimes have identical larvae and since the same species apparently may have two different larval forms, it is not unreasonable to suppose that mutations could affect the form of either larva or adult independently of each other.

MATERIALS AND METHODS

Adult colonies were kept in darkness over night and until the experiments were begun. After exposure of the parental colonies to light, the photopositive larvae released by illumination were easily pipetted to experimental vessels. Generally a single group of adult colonies yielded enough larvae for experiments on several different days. For observations on the geotropism of the larvae and their reactions to light, small vials 1.5 cm. in diameter and 8 cm. high, as well as stender dishes were employed; for microscopic examinations stender dishes and occasionally well slides were used. When slides were used, they were covered to prevent evaporation, which hastens setting by increasing the salinity. A box, 5 by 5 by 15 cm., covered with black paper on all surfaces except the exposed side, was used for experiments on the effects of colored lights.

The Reactions of the Larvae to Light, Heat and Gravity

Diffuse daylight. As described by Grave (1930), the larvae are intensely photopositive during the first three or four hours after their release from the ovicells and then become photonegative. The writer found the photonegative reaction to be somewhat more intense than that described by Grave (1930), who concluded that "it might be overlooked" because of its gradual onset. By 6-8 hours both species of larvae were always definitely photonegative and this reaction was intensified by placing them in sea water diluted by 50 per cent. Furthermore, they changed their reaction from positive to negative immediately after they were placed in sea water buffered to a pH of 9.6 (borate buffer) or diluted by 50 per cent, even when the latter was made hypertonic by the addition of sucrose. In sea water containing 2.5 mg. of copper chloride per liter the majority of the larvae, still photopositive 30

minutes after exposure, did not swim towards the light when the dish was reversed as they normally do. When a concentration of 5 mg. copper per liter was used, they became photonegative within 30 minutes. Even 0.5 mg. per liter reduced the intensity of the photopositive reactions. Since these peculiarities were not observed when the organisms were ejected from a pipette into sea water, mechanical force can hardly be the cause of this reaction. The absence of photic responses in mixtures of sea water and magnesium chloride was mentioned in a previous paper (Lynch, 1949).

Reactions to blue and red light. When a prism spectrum was used to illuminate vials placed horizontally in a black box about 16 feet from a 500 watt bulb, the larvae aggregated densely in the yellow, orange and red regions during their photopositive phase but afterwards congregated in large numbers (80-90 per cent) in the dark region beyond the violet when only the middle portion of the vials was illuminated, or in the violet region when the whole tube was exposed. Apparently this behavior was merely a response to heat, which the larvae tried to avoid, or to light intensity rather than to color.

Since the above method was unsatisfactory, the remaining experiments were carried out with blue and orange-red Eastman Kodak Wratten filters, numbers 76 and 72 respectively. Number 76 transmits a wavelength of approximately 4200-4800 Å and number 72 a wavelength of 5800-6600 Å. These filters have nearly equal relative energy transmission when illuminated with a 400 watt bulb according to Hecht (1921). One end of the vials was illuminated by blue light and the other by red. In the center there were two dark bands caused by the opaque paper of the edges of the two filters where they touched each other. More specimens attached in these dark regions than in either the blue or the red end; these, of course, were not counted in the total number that responded to the colored lights. Of the 292 larvae used in 5 trials 67 per cent attached in the red end. Actually, due to errors in counting large numbers of larvae often attached one on top of the other, the percentage was probably larger than this. In four of the trials there were 1.5 to 2 times as many in the red end. The standard error of the proportion was obtained from the formula, $S.E._p = \sqrt{pq/N}$, for calculating the significance of the results. If it is assumed that the null hypothesis holds in this case, the expected percentages in each end would be 50 per cent (.50), and both p and q would equal .5 each. Thus the $S.E._p = \sqrt{(.5 \times .5)/292} = .0291$. Since an excess of .17 (67 per cent minus 50 per cent) over that postulated by the null hypothesis is at least five times the $S.E._p$, the results would fall easily within the range of "very significant." In these experiments *B. flabellata* showed as much uniformity of response as *B. turrita*, despite the absence of eye-spots on the former. Visscher (1927) obtained somewhat similar results with colored tiles, for more Bryozoa attached to red test panels than to green, black or yellow ones, and no settings occurred on the white ones. (Cf. also Edmondson and Ingram, 1939.)

Darkness. As Grave (1930) had observed, darkness delays fixation and favors attachment to the surface of the water. The writer found the larvae of *B. turrita* to be almost universally active at the end of 24 hours, when kept in complete darkness in a microscope case, and the majority continued to swim for three or four days (the normal duration of the natatory period of most larvae of this species does not exceed 24 hours). Specimens kept in bottles remained active longer than those

in uncovered syracuse dishes. Since the sea water in the latter became more concentrated by evaporation, the increased salinity hastened metamorphosis. (Cf. Lynch, 1947). By six days the attached organisms had elongated considerably (maximum length, 1.45 mm.), giving the surface of the water a fuzzy appearance; this was caused by a great abundance of transparent material, much of it in the form of four, symmetrically placed stolons for attachment to the surface film and the remainder organized into a club-shaped structure joined to the stolons and containing in its center an opaque spherical mass that closely resembled the unmetamorphosed larva. The eye-spots were generally visible either in the opaque mass or at a short distance from it in the transparent parts. Apparently development ceased after elongation, for polypides were never observed.

Effects of temperature. Heating the medium to 30° C. accelerated metamorphosis, and raising the temperature to 32–35° C. caused cytolysis; both effects were more pronounced in *B. turrita* than in *B. flabellata*.² Many of the former, mere rings of ciliated tissue without material in their centers, were often observed swimming slowly in test tubes exposed to light from a 500 watt incandescent bulb. Enormous amounts of adhesive material always surrounded the larvae after extrusion of the hold fast, but rigid attachment failed to occur. Expansion, especially by elongation along the apico-basal axis, followed exposure to heat. Sausage-shaped streamers of tissue from the pallial furrow, similar to those produced by exposing the larvae to sea water containing an excess of magnesium chloride (Lynch, 1949), were extruded by the larvae of *B. flabellata* from their apical ends, which always looked larger than normal. Development was poor or totally lacking in both species, even when cytolysis did not occur. Marcus (1926) briefly mentioned the accelerating effect of heat on bryozoan larvae.

Gcotropism. When diffuse daylight enters a test tube of sea water horizontally, the larvae become fixed at various places along the side farthest from the window, although attachment to the surface is also very common. Under experimental conditions the larvae generally fell to the bottom just after immersion in a new medium, especially if it contained an excess of various salts. When sea water was mixed with equal parts of normal solutions of sodium, potassium, magnesium or calcium chlorides, the larvae did not swim to the surface again, apparently because ciliary action was too feeble. In mixtures of 80 cc. sea water per 20 cc. of normal calcium chloride, however, vigorous swimming movements were maintained. Heating the medium to 30° C., keeping the larvae in darkness or immersing them in 80 cc. sea water per 20 cc. normal sodium chloride favored attachment to the surface. This concentration of sodium chloride, however, affected the two species somewhat differently. Since *B. flabellata* metamorphosed almost immediately in this mixture most of the larvae did not recover sufficiently from their initial "fright-reaction" to reach the surface, and floating larvae were not often observed; *B. turrita* re-

² Experiments on *B. neritina* had shown that a reduction of temperature from 23° C. to 7° C. caused all the larvae to become geopositive and lengthened the natatory phase by 2–3 hours (Lynch, 1947, p. 128). Since the writer was not interested in lengthening the larval phase of the Woods Hole species, similar experiments were not repeated. It cannot be assumed, however, that the results would have been similar, since Barrois (1879) reported that a bowl-full of Serialaria (Ctenostomata) that invariably attached at night, was placed in ice and maintained at a temperature near zero all night. Contrary to his expectations, setting took place in a normal manner.

mained active longer and many were at the surface when fixation took place. During the photonegative phase the larvae of *B. flabellata* swimming in normal sea water could be made to move downward by placing the light source above them or upward by illuminating them from below. (Cf. also Grave, 1930.) It seems likely, therefore, that in this species the positive geotropism that occurs in nature towards the end of the matatory period is brought about both by light and by a reduction in ciliary movement. In this respect the species at Woods Hole differ considerably from *B. neritina*, for geotropism in the latter is apparently independent of phototropic responses.

DISCUSSION

The experiments just described and those presented in former papers (Lynch, 1947, 1949) show that heat, light, salinity and the relative proportions of ions in sea water can profoundly affect the natatory period of *Bugula* larvae and the subsequent growth of zooids. From an ecological standpoint, environmental fluctuations that affect the setting of larvae are of paramount importance. Hutchins (1945), having observed that adult species of Bryozoa grew quite well after being transplanted from their natural habitat to one where they were either rare or totally absent, concluded that "in all probability the critical tolerances of environmental variations are those of the larvae, particularly during metamorphosis when they may be supposed to be minimal." An interesting problem is posed by the peculiar distribution at Woods Hole of the two species of Bryozoa under discussion. Grave (1930) stated that *B. turrita* is found in Vineyard Sound, but not in the Eel Pond, whereas *B. flabellata* is abundant in the Eel Pond, but is not ordinarily found outside it, even though the two bodies of water are less than 300 feet apart and communicate freely with one another.³ Although the adults when transferred from one region to the other on a raft may live for a few months or a year, all efforts to establish new colonies by the transplanted species have so far met with failure (Grave, 1930). A similar peculiar distribution of *Teredo navalis* and of certain hydroids can also be observed. What explanation can be given for these facts? That the larvae are extremely sensitive to the ions present in sea water is evident; whether they can complete metamorphosis and attain normal growth depends upon a very delicate balance of the chemical constituents of their environment. There are, however, so many variables affecting larval behavior that it is extremely difficult to isolate specific ones as causative agents of ecological distribution. Conceivably a particular species thrives best under conditions that enable the organism to terminate larval life after an optimum swimming-time, since larvae that are induced to swim long beyond the normal time of setting rarely develop or form zooids comparable to the controls in size or differentiation. Species such as *B. neritina* with an extremely short natatory period under laboratory conditions seem to be more adversely affected than those whose larval life is of longer duration. It may be that stored nutritive material essential for the formation of zooids is exhausted by prolonged swimming.

The behavior of the two species of *Bugula* from Woods Hole shows certain marked similarities to that of *B. neritina* (from the Beaufort region) and a few

³ He referred, of course, to the natural habitat of the two species. Actually both species were found by the writer growing on a raft at the entrance to the Eel Pond (August, 1949).

striking contrasts. Their reactions to excesses of various metals are nearly identical (Lynch, 1947, 1949). (Copper, however, was not tried on *B. neritina*.) But there are significant differences in their responses to light and gravity. The larvae of *B. neritina* never have a photonegative phase at any time under laboratory conditions, although there is some evidence that they become indifferent to light just before setting. In this respect they resemble the European variety of *B. flabellata* described by Nitsche (1870). Furthermore, they almost universally remain near the surface, and up and down movements in a vial occur but rarely. The larvae of both species from Woods Hole, however, swim vertically along the side of the container during their photonegative phase as readily as they do horizontally during the transitional period when their phototropic responses are beginning to reverse.

The marked similarity in both phototropic and geotactic behavior of the two species from Woods Hole and the contrast that exists between the behavior of these species and that of *B. neritina* would suggest the possibility that environmental conditions in the two regions might be partially responsible for differences in behavior. Both the extreme brevity of the natatory phase of the Beaufort species and the failure of the larvae to become geopositive at any time under laboratory conditions would seem to be influenced at first sight by two obvious differences in environment, a higher temperature and a brackish condition of the water. This hypothesis is based on the experimental evidence that extreme variability of the duration of the natatory period of a given species can be brought about by altering the ionic balance of the medium, by changing the salinity or by varying the temperature. By altering these factors the geotropic behavior of the larvae can also be changed. Since the abundance of oysters in the brackish waters of Beaufort would suggest the probability that the copper content of this region might be greater than it is at Woods Hole, it would not be unlikely that this ion, capable of hastening the onset of metamorphosis in several sessile organisms, might be largely responsible for the extreme brevity of the larval stage of *B. neritina*.⁴ The hypothesis that a greater concentration of copper in the Beaufort sea water and the higher temperature prevailing in that region might play a role in causing contrasts in behavior of the northern and southern species is not illogical, since the natant phase of *B. flabellata* can be shortened appreciably either by adding CuCl_2 to sea water or by raising the temperature of the medium. Furthermore, warming the sea water to 30° C. favors surface attachment of *B. flabellata*, whereas cooling the medium causes the larvae of *B. neritina* to become geopositive and prolongs their larval stage; thus, either species may be made to react like the other in this respect. Apparently the pelagic habits of *B.*

⁴ In brackish waters, according to Prytherch (1934), the copper content may reach a concentration of 0.1–0.6 mg. per liter during low tide, whereas it rarely exceeds 0.02 mg./liter in the sea (Galstoff, 1943). Likewise the relative proportions of sodium, magnesium and calcium in brackish waters differ considerably from the distribution of these ions in the ocean, since the order of concentration of these ions approaches that of fresh water (calcium, magnesium and sodium). (Cf. Clarke, 1924.) Recently (after this paper had been prepared in its present form) Glaser and Anslow (1949) gave the copper content of Woods Hole sea water (spectroscopically determined) as $2.50 \pm \times 10^{-7}$ M Cu. They found that a sample of Beaufort sea water had a value as high as 1×10^{-6} M Cu; they noted, however, that the latter may have been contaminated (p. 127 and 128).

neritina are correlated with their brief natatory period (Lynch, 1947);⁵ likewise the much more frequent occurrence of geopositive settings of *B. flabellata* under normal conditions seems to be related to their naturally longer larval phase, for the number on the bottom of a vessel begins to increase after the larvae have been active for several hours.

Nevertheless, even though the behavior (except phototropism) of one species can be duplicated almost exactly in the other by altering the environment, neither differences in temperature *alone* nor in the content of the sea water can account for contrasts in the behavior of the northern and southern species. The monthly mean temperatures during July and August at Woods Hole and at Beaufort differ by only six or seven degrees, according to McDougall (1943), and experiments performed at Beaufort by the writer showed no marked change in the behavior of *B. neritina* when the temperature was reduced to 21° C. (the monthly mean for Woods Hole), although a more drastic reduction of temperature did reverse the geotropism of the larvae and prolong their free-swimming phase. Likewise, when larvae of *B. flabellata* were immersed in sea water taken at low tide from the Beaufort region and shipped to Woods Hole, their behavior was like that of the controls. No shortening of the larval phase was observed. (The experimental sea water had a pH of 7.5 when used.) Logically, negative results were partially predictable, since previous experiments had shown that a concentration of copper chloride as low as 0.5 mg per liter of sea water (about maximum for brackish waters) had no appreciable effect in shortening the natatory period, although higher concentrations were effective.⁶ Is it then a mere coincidence that the southern species with its short natant phase lives in an environment where two factors, a higher temperature and a presumably (?) greater concentration of copper, are both present and either of these can accelerate the onset of metamorphosis? There are two possibilities. On the one hand, since experimental modifications of temperature that proved to be effective in lengthening or shortening the larval phase were more drastic than those actually prevailing in nature and since the same was true of the copper content, conceivably slighter changes of both factors combined might be as effective as more extreme alterations of each one separately. It should be noted that, since the temperature of the Beaufort sea water was not raised to the degree ordinarily prevailing in that region, the environment of the southern species was only partially duplicated on the northern one. On the other hand, since there are generic and specific as well as individual differences in the natatory phase of bryozoan larvae, it seems more tenable to assume that species genetically determined to have a short larval period can thrive only in an environment where ions, presumably requisite for setting, can be rapidly absorbed. Conceivably, there may be specific differences in the ion-absorbing ability of larvae. This assumption, however, offers no explanation for the fact that the larval phase of the majority of a given species may end at two hours on one day and at ten hours on another.

⁵ By using two sets of data that appeared to have the least positive correlation, the coefficient of correlation between the number of larvae of *B. neritina* that were kept active for four hours by a reduction of salinity and the number that became geopositive at the time of setting was found to be +.53 and +.57.

⁶ It should be noted that concentrations of CuCl_2 as high as 1.25 mg. per liter had no effect; Prytherch (1934) found that in his experiments virtually all the copper was precipitated when less than .5 mg./liter was used.

(See Table I, p. 30, Lynch, 1949).⁷ Before the relative effects of environment can be evaluated it is necessary to know whether there are significant differences in the length of the natatory period of the same species in different localities. Since Edmondson and Ingram (1939) reported that larvae of the Hawaiian *B. neritina* attach at night as readily as during the day, it may be that these organisms have a much longer natant phase than the ones studied at Beaufort. The latter (laboratory conditions) were always released a short time after exposure of the parental colonies to light, and active unattached ones could rarely, if ever, be found after noon. Caution must be observed, however, in making such an assumption, for it is unwise to conclude that the natatory period of larvae under natural conditions is as brief as it is in the laboratory. Indeed, the vertical distribution of adults indicates that in nature these larvae are probably active longer than an hour or two (maximum time in the laboratory) and undergo sufficient activity to make most of them geopositive. It would be extremely valuable to have definite information regarding the behavior of *B. neritina* on the California coast. There is also need for further research on the interaction of factors capable of accelerating or retarding metamorphosis. Some may have antagonistic effects; others may act synergistically.

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SUMMARY

1. The larvae of both *B. flabellata* and *B. turrita* are photopositive in diffuse light during the first 3-4 hours after release from the ovicells and then become photonegative. They became photonegative immediately, however, when they were placed in sea water buffered to a pH of 9.6 or diluted by 50 per cent; sea water containing copper chloride either reduced the intensity of the photopositive phase or caused a reversal of phototropism depending on the concentrations that were used. These organisms became indifferent to light in mixtures of 80 cc. sea water per 20 cc. of either normal calcium chloride or magnesium chloride.

2. Larger numbers of larvae attached in the red end of a test tube illuminated by red and blue light passing through Wratten filters than in the opposite end.

3. Heating sea water to 30° C. hastened metamorphosis and favored surface attachment, but development was poor or entirely lacking at this temperature. Darkness delayed metamorphosis and also caused attachment to the surface film;

⁷ Barrois (1879) stated that in the laboratories at Roscoff the same species of Bryozoa generally showed extreme variations of the natatory period on different days and that cases of this strange phenomenon could be found in all groups but was especially striking in *Pedicellina* and *Cyphonauts*. In some cases (*Flustrella hispida*, especially) he found it impossible to obtain a single fixation during a period of many weeks, even though the larvae were very abundant. At other times, under apparently identical conditions, fixations took place in large numbers. He noted that the incapacity of larvae to fix themselves might persist for a long time or cease suddenly. At times settings occurred in various parts of the bowls; at other times they took place *en masse* at certain points. But these anomalies were entirely absent in bowls prepared at the same time and place and under identical conditions. Harmer (1922, p. 513), likewise, noted the difficulty of persuading larvae to attach under laboratory conditions and stated that it could be surmounted by placing adult colonies in a vessel closed with fine muslin and left attached to a buoy or placed in a deep tide-pool. Evidently environment is extremely important.

development ceased after a fair amount of growth and a slight degree of differentiation.

4. In mixtures of equal amounts of sea water and normal solutions of sodium, potassium, magnesium and calcium chlorides the larvae became geopositive on entering the medium and remained so during the experiments.

5. Some ecological problems of the distribution of three species of *Bugula* are discussed and tentative suggestions for their solution are offered.

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